# HIPPOCAMPAL EEG AND MOTOR ACTIVITY IN THE CAT: THE ROLE OF EYE MOVEMENTS AND BODY ACCELERATION

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In cat the relation between various behaviours and the spectral properties of the hippocampal EEG was investigated. Both EEG and behaviour were quantified and results were evaluated statistically. Significant relationships were found between the properties of the hippocampal EEG and motor acts (walking, sitting, eating, stepping and eye movements). These results were compared with those obtained in dog under similar experimental circumstances. Species differences were found particularly regarding the fact that in the cat a dissociation between frequency and amplitude parameters was obtained for some behaviours; this may explain why appreciable differences in the visual interpretation of EEG records of different species are often reported. A simple model of the modulation of hippocampal EEG by brainstem inputs is presented. Particular attention is paid to species differences regarding the anatomy and physiology of the pathways involved in this modulation. It is concluded that in cat a strong relation exists between the modulation of spectral properties of hippocampal EEG and vestibular inputs and/or eye movements. The effects of body acceleration on hippocampal EEG are put in evidence and related to theories of hippocampal function.

## INTRODUCTION

The most prominent feature of the electrical activity of the hippocampus in mammals, is the so-called rhythmic slow activity (RSA) or theta rhythm. The basic neuronal mechanism responsible for the generation of RSA is located in the medial septum[21,22]. The septum receives inputs from the diencephalon which depend upon neuronal activity in the brainstem reticular formation. The higher the impulse density in these inputs the higher, within certain limits, the frequency and the amplitude of the RSA component in the hippocampus EEG; at high input densities the RSA amplitude decreases and desynchronization (small amplitude irregular activity), (SIA),

occurs[20]. Essential in this context is the notion that can be derived from the investigations of Paiva et al.[20] and Arnolds et al.[2] that RSA behaves as a graded variable which may assume a whole range of possible values as regards frequency and amplitude (cf. also the comment of Komisaruk and Semba in ref. 30). The fact that the frequency is a sensitive index of the modulation of the hippocampal EEG with behaviour has, since the studies of Lopes da Silva and Kamp[18] and Vanderwolf[29], become well established. Thus the spectral properties of RSA are related to certain aspects of behaviour.

Ever since this was recognized, attempts have been made to adequately define the set of behaviours 'related to RSA' and define their com-

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mon characteristics. At the same time it has been a matter of debate whether this relation is identical for all mammals investigated, namely rat, mouse, Mongolian gerbil, guinea-pig, cat, dog and various primates[23]. For the rat the relation between overt behaviour and hippocampus EEG has at present been described in an objective and quantitative way by Vanderwolf and others[29-32]. Essentially they state that reflex and consummatory behaviours such as eating, scratching, pelvic thrusting, called 'automatic' behaviours by these authors, are accompanied by large amplitude irregular activity (LIA) and in some cases by low frequency RSA, while 'voluntary' movements that do not occur in such a stereotyped pattern (head movements, swimming, walking, jumping) are related to RSA of a higher frequency.

The same behaviour pattern may be related to higher or to lower RSA frequencies and amplitudes depending on its physical characteristics. For example, locomotion may take place at various speeds, related to the muscular force exerted. Arnolds et al.[3] showed that in the dog low walking speeds are related to lower values of RSA frequency, amplitude and rhythmicity than high speeds. In a very fast running rabbit RSA was seen to change into SIA[17]. This implies that for some behaviours a relationship exists between 'muscle force' and the spectral properties of the concurrent hippocampal EEG.

Some observations in the cat might lead one to believe that in this species the relationships between hippocampus EEG and behaviour differ markedly from those found in the dog and rat. Some investigators, for example Whishaw and Vanderwolf[35], Kemp and Kaada[16], relate 'fixed staring' to clear RSA, whereas the RSA concurrent with 'exploratory walking' was of lower amplitude and less regularity. Frederickson et al.[11] also reported RSA during immobility in cat and noted that RSA in cat is of variable and often quite small amplitude during locomotion[12]. Yet Whishaw and Vanderwolf[35] found a continuous RSA with a frequency of about 5 Hz in cats walking on a conveyor belt. The experimental data on the cat are at present rather patchy; owing to an overall lack of quantitative data on hippocampal EEG and behaviour in cats it is difficult to make comparisons among different studies and with data from other species. Another difficulty in the interpretation of the data available on the cat is the fact that most EEG derivations used were bipolar from closely spaced electrodes. In view of the possibility that different phase relations may exist between signals picked up by the two tips of a bipolar electrode, depending on the animals' behavioural state[6,9,13,37,38] a judgement about the presence or absence of RSA in such EEG-records can be ambiguous.

We investigated, for a number of well defined behavioural situations, the related RSA in the cat along the same lines and with the same techniques of analysis and quantification we used in the dog. In this way we expected to get a clearer picture of the position of the cat among the other mammals, with respect to this brain–behaviour relationship. Such a comparative physiological and behavioural approach may, moreover, provide essential elements for formulating a generally valid model explaining the relationship between RSA and behaviour.

MATERIALS AND METHODS

*Electrodes and their placement*

Under general anaesthesia, 5 cats, referred to as B, E, F, J, L, were chronically implanted with electrode bundles made of a number (4–7) of intertwined stainless steel wires of 100 μm diameter, insulated to 0.3 mm from the tip and with intertip distances of 0.9 mm. These bundles were aimed at the dorsal hippocampus using standard stereotaxic techniques[27]. All electrodes were soldered to a plug, fixed to the skull with dental cement.

In all cats a number of signals were recorded as indicators of behaviour. In order to monitor sniffing two intertwined stainless steel electrodes were implanted in the olfactory bulb. A stainless steel pin was driven into the skull above the visual cortex to record waves associated to saccadic eye movements, the so-called ponto-geniculo-occipital or PGO waves[7,8]; in our case only surface-positive waves over the occipital cortex were recorded. Another eye movement indicator was obtained by implanting, bilaterally, stainless steel
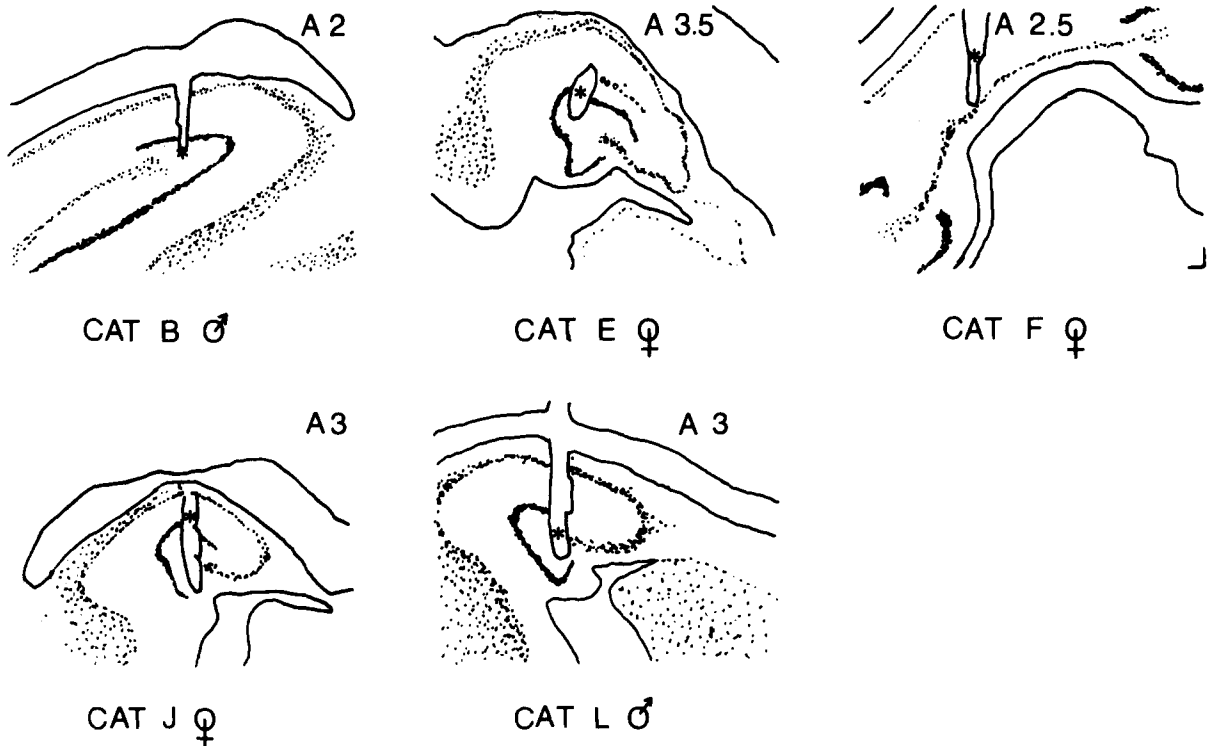
Fig. 1. Position of the electrodes (marked with *) from which the EEG signals used for analysis in this paper were derived. The symbol A ... given in the upper right hand corner of each drawing refers to the section in the Atlas of Snider and Niemer[27] that most resembles the particular histological section.

wires at the back of the eye sockets. Moreover each cat was provided with 4 chronically implanted EMG electrodes, one in the triceps of either forepaw, the other in the M. cleidomastoideus or M. sternomastoideus on either side of the animal's neck. These electrodes consisted of teflon-insulated multi-strand stainless-steel wire. About 10 mm of the insulation was removed and this bare end was sutured onto or into the exposed muscle. The wires were then led subcutaneously to the skull of the animal and fixed to the plug.

*Recording*

All derivations were to one common electrode, a stainless steel pin, placed in the frontal bone, at the level of the frontal sinus. EEG, EOG and EMG signals of interest were transmitted by means of a 16- or a 20-channel radiotelemetry system[15]. On the male connector plug of this telemetry system a miniature accelerometer was mounted, in such a way that the vertically oriented component of acceleration was detected. The

output of this device was transmitted telemetrically as well. These signals were further amplified by a 16-channel EEG machine (Elema) and recorded on a multi-channel analogue tape-recorder (Ampex) together with digital signals marking certain events (such as the moment at which the animal obtained a reward) and a digital time code. All these signals were written out on paper.

For computer analysis the hippocampal leads that upon visual inspection appeared to yield the larger amplitudes and more regular RSA were selected. The post-mortem histological verification of these electrode positions is illustrated in Fig. 1. Clearly the criteria used in selecting signals for analysis favoured placements in the dentate area as is to be expected on the basis of studies by Holsheimer et al.[13], Winson[37,38] and Bland et al.[6].

*Computer processing*

A computer system was used for the analysis of

relationships between behavioural data and spectral EEG parameters. As primary EEG data we used the amplitude spectrum of the EEG generated by a series of 1 Hz bandwidth band-pass filters, ranging between 2 and 14 Hz in resonance frequency. The output of these filters was rectified and smoothed, using a circuit with a 0.25 s. time constant. Each 200 ms these were sampled and a spectrum stored in the computer. From these spectra we derived 3 spectral parameters: an index of peak frequency ($I_{PF}$) which essentially corresponds to the frequency at which the largest spectral amplitude is found weighted by the amplitude values of the neighbouring spectral lines, the amplitude in a 3 Hz wide band around the peak frequency ($I_{AM}$) and an index of rhythmicity ($I_R$) which is found by dividing the amplitude within the 3 Hz band around the peak frequency by the amplitude of the other spectral components[2]. The use of these spectral parameters is based on the assumption that a peak is present in the theta band of the power spectrum. Basically the computer selects the filter with the highest output amplitude between 2 and 10 Hz and assigns the corresponding resonance frequency as the peak frequency. Thereafter the computer calculates the 3 indices introduced above. For a full account of the analysis system and of the detailed description of how these indices were computed the reader is referred to Arnolds et al[2]. Signals without a clear spectral peak or a peak lying outside the range 2–10 Hz may yield dubious spectral indices. This problem did not occur in our studies on the dog, since in this species a significant rhythmicity in the theta range is present under practically all behavioural circumstances[2]. In cat this is not always the case.

Time-locked to the sampling of the EEG spectra a number of behavioural parameters was recorded. As such we used the rectified and smoothed output of the accelerometer (ACC), the movement transducer of the treadmill, EMG, EOG, visual cortex or olfactory bulb electrodes. It must be stressed that only $I_{PF}$ and $I_R$ are normalized quantities. $I_{AM}$ as well as all behavioural parameters are not normalized.

A system of averaging programs was used to determine the value of EEG and concurrent behavioural parameters recorded during a number of realizations of the same type of behaviour, and then to compute the average value of these parameters. Each realization of a certain behavioural state had a minimum duration of 0.4 s. In order to make sure that the data used in these averages concerned spectra with a clear peak in the theta-range $I_R$ was required to be $> 0.36$ under all circumstances. Periods that did not comply with this criterion were rejected. The fact that for each behavioural state and for each EEG or behavioural parameter a number of realizations of the same behaviour were available, made possible the statistical comparison of parameters recorded during different behaviours. To this end a non-parametric test (Wilcoxon matched-pairs signed-ranks test[26]) was employed. This type of analysis will be referred in the present context to as 'epoch analysis'.

It was also possible to determine the average value of each EEG or behavioural parameter as a function of time, in relation to a certain trigger-point. In order to determine the significance of the variations in the parameters in the course of time the sign test was used. This type of analysis will be referred to as 'time course analysis'.

All analyses presented are based on a randomly chosen set of instances of the same behaviour, drawn from a single experimental session. Only the occurrence of artefacts precluded a record from being used.

RESULTS

*General*

The experiments will be described in 4 sections. Results obtained from cat are compared to the equivalent data obtained from dog, described in detail in Arnolds et al[2-4].

*Experiment 1: 'Fixed staring', PGO waves and RSA*

Since RSA during 'fixed staring' has been put forward as indicating a dissociation between RSA and movement in the cat[16], we investigated whether during 'fixed staring' subtle forms of movement, particularly of the eyes, could be shown to be related to hippocampal RSA. Eye movement records were collected from the

periods of sitting still that occurred under the conditions of experiment 3.

Triggering on separate PGO waves, we observed a clear-cut increase in $I_{PF}$ related to the eye movement (Fig. 2). $I_{AM}$ and $I_R$ showed negligible small increases related to PGO waves. The
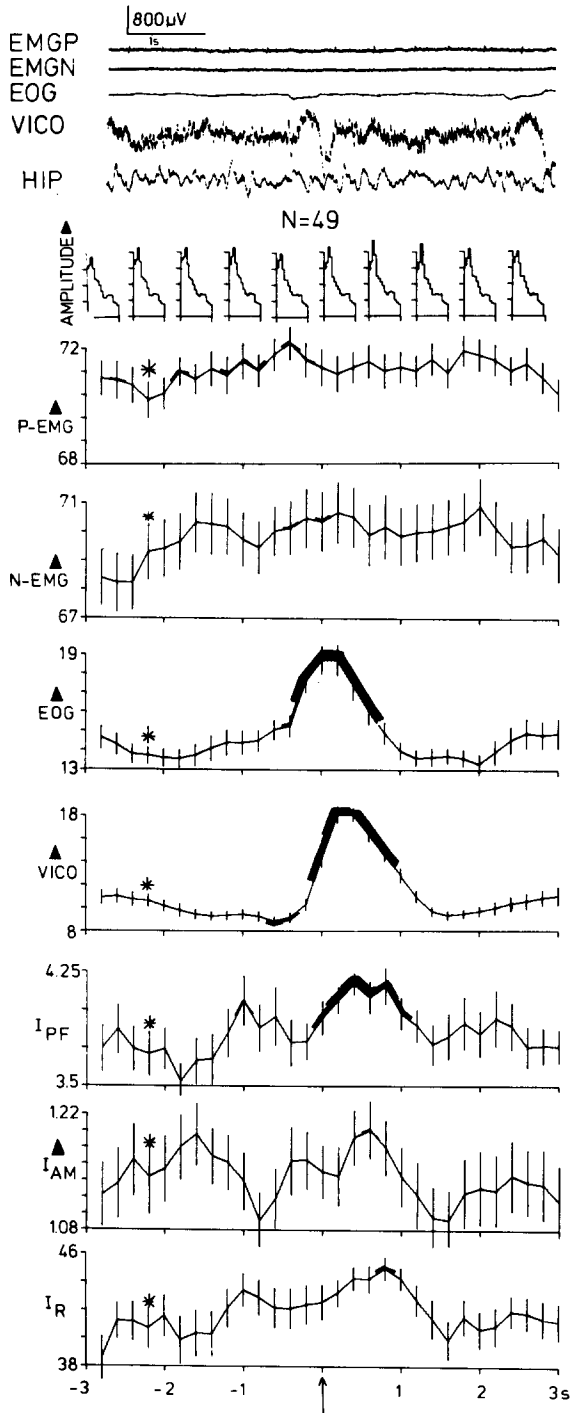
variations that occurred in the paw-EMG parameters appeared to have no relation to either the PGO waves or the variations in the spectral parameters.

From these findings it may be concluded that in the behavioural state described as 'fixed staring', in cat, the RSA spectral characteristic particularly the frequency index is in any case influenced by the occurrence of eye-movements. Thus the relation between eye-movements and RSA observed during REM-sleep by Sakai et al. in the rat[25] can be extended to the awake cat.

### Experiment 2: riding on a cart (passive translation)

### Procedures

One of the most effective ways of eliciting RSA in dog is by means of body acceleration during passive translation in a cart[3]. In order to investigate whether a similar phenomenon could also be obtained in the cat, cat B was placed in a hammock fixed to a cart in such a way that the paws of the animal were free from the floor. The cart carrying the cat was driven by the experimenter over a straight runway of approx. 14 m length, starting from a standstill position to an approxi-



Fig. 2. Time course analysis of the spectral properties of the hippocampus EEG and of the value of 4 behavioural parameters triggered by PGO waves (arrow). P-EMG, paw EMG; N-EMG, neck EMG; EOG, electro-oculogram; VICO, visual cortex EEG; HIP, hippocampal EEG, recorded from cat F. In the top section of the figure 5 traces, taken from a single trial are reproduced. Under the EEG trace a series of histograms represent the average (n = 49) running spectral analysis of the hippocampus EEG in a number of 200 ms time-bins preceding, at, and following the trigger events. The placement of the spectra corresponds to the time scale of the curves. The lower section consists of a number of curves representing the time course of EEG and behavioural variables in relation to the trigger. The bar through each data point represents the standard error of the mean. Where the curve is thickened there exists a statistically significant difference between that part of the curve and the value indicated by an asterix, chosen as a point of reference (sign test). The thicker the line, the higher the significance level. In any case $P < 0.05$. The highest degree of thickening indicates $P < 0.001$. N indicates the number of averaged events. $I_{PF}$ is the index of frequency; $I_{AM}$ is the index of amplitude in arbitrary units; $I_R$ is the rhythmicity index (see text for definitions). Note the increase in the values of spectral parameters, particularly $I_{PF}$ in relation to PGO waves.

mately constant speed of about 3.5 m/s. Care was taken that the animal was motionless at the beginning of each trial. After each run the cat was given some dry food. Thereafter the cat was driven in a backward direction to its starting position in a slow and irregular manner. Cat E was subjected to the same procedure, but was trained to sit in a box on top of the cart. In this position it was driven along the runway in the same way as described above. The driving speed was monitored by means of a photocell 'looking' at a black and white stripe pattern on the floor over which the cart was pushed (each stripe 10 cm wide). The signal generated by the photocell was transmitted and recorded along with the other behavioural parameters.

*Results*

At the start of each run, when the acceleration was maximal, both cats showed some movements of paws and neck. These movements were very slight and no stereotyped pattern could be discerned. In fact the EMG records give a more distinct impression of these movements than could be obtained by means of visual observation. These reactions appeared to habituate as the session went on. Apart from these slight movements at the beginning of each trial, the cats kept quite still as they were driven along. The paw EMG of cat B showed a transient rise at the beginning and at the end of each ride, cat E showed a tonic increase in EMG activity during the whole ride (Fig. 3). This figure shows also that the EOG activity increased during the cart ride; the increase in the integrated activity of the olfactory bulb indicates a change in the pattern of respiration in the course of the ride. EEG changes were characterized by an increase in frequency ($I_{PF}$) during the whole ride, both in the forward and the backward direction, while the amplitude $I_{AM}$ of the hippocampal EEG showed a transient decrease at the start of each ride (Fig. 3). No consistent statistically significant changes in $I_R$ were noted. In both cats we computed average values for spectral and behavioural parameters during periods of 'cart ride forward', 'cart ride backward', 'sit still in cart' and 'eat in cart'. The results are virtually identical for both cats with
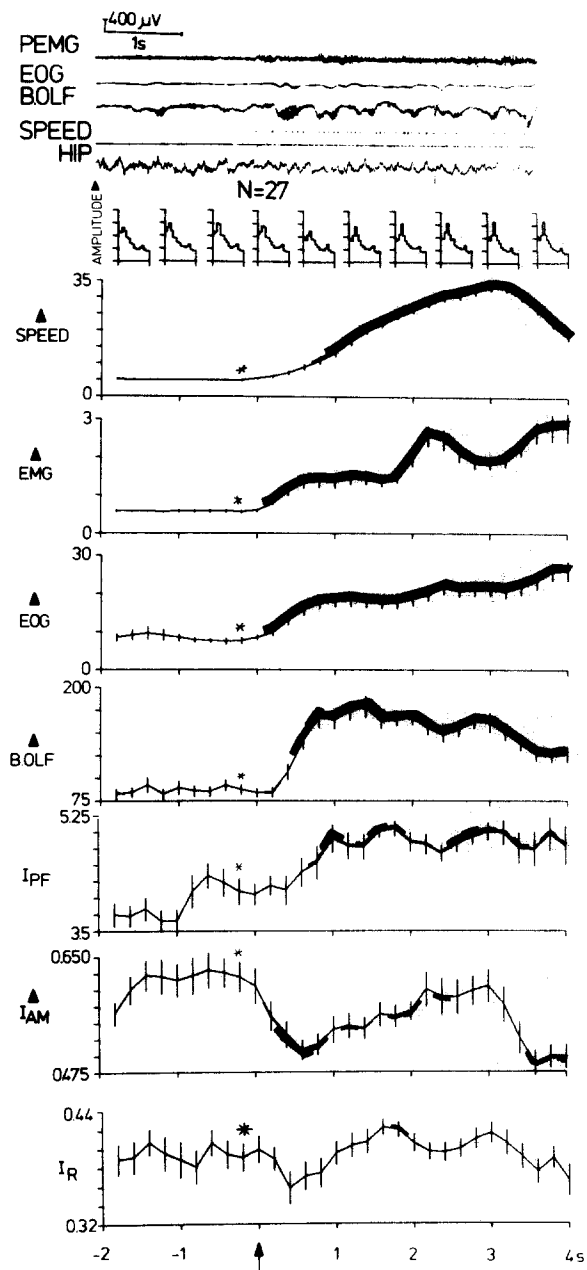


Fig. 3. Time course analysis of the spectral properties of the hippocampal EEG, of the integrated bulb activity and of the value of 3 behavioural parameters triggered by 'start cart ride'. PEMG, paw EMG; B.OLF, olfactory bulb EEG; SPEED, indication of cart running speed. Note dip in $I_{AM}$, followed by an increase in $I_{PF}$, upon start of cart run (see also caption of fig. 2).

respect to $I_{PF}$ and $I_{AM}$. For neither of the parameters was there a significant difference between riding fast forwards (cart ride in Fig. 4) and riding more slowly backwards (ride back). Nor was

there a significant difference between eating and sitting still in cart. However, the peak frequency of the hippocampal EEG during both types of riding was significantly higher than during sitting or eating. The amplitude was significantly lower during eating than during all other behavioural states (Fig. 4).

*Experiment 3: Modulations in gross motor behaviour (active translation)*

Since RSA typically occurs related to overt movement it was of interest to determine in a quantitative way how the characteristics of RSA in cat change in relation to well defined motor acts.

*Procedures*

All animals were studied while performing the task decribed below. The cat was strapped into a classical treadmill in which it could walk overground in circles of 2.6 m in diameter. The attachment of the animal to the arm of the mill was such that it retained a considerable freedom of movement (it could freely sit, lie down, walk forwards and backwards, turn around and move its head). This set-up allowed displacement to be measured with a resolving power which is equivalent to a displacement of $\pm 2$ cm. Using a photo-electric device an electrical pulse was generated each time the treadmill was displaced 2 cm; these pulses were displayed as function of time as shown in the upper part of Fig. 5 (Mill). The treadmill was placed in a room of approx. 50 m$^2$. In one of the corners of the room a food dispenser was placed in such a way that the cat, attached to the mill, could easily reach the food dish. The animals were taught to walk around once in the treadmill and to stop at a point near to the food dish. It was required that the cat should sit still at this point for a period of 10 s or longer. If walking and sitting had been performed to satisfaction of the experimenter, the food dispenser was activated. It then produced two click sounds with an interval of 3 s. At the second click two or 3 pellets of dry food fell into the food dish. The cat would eat these and set forth on its next round in the mill. While in training the animals were entirely depen-

dent upon the rewards earned during these experiments for their daily food allowance.

*Results*

All cats were able to perform the task as described. None of the cats attained, however, a continuous, highly concentrated 'automaton-like' performance of the task, as could be seen in the dogs we studied previously. During their walking periods the cats appeared to remain alert to any outside stimulus. This was not evident in the dogs we studied.

In Fig. 5 a time course analysis is given of behavioural parameters during the performance of the task described above; note the increase in all spectral parameters when the cat is walking, and their decrease when stopping. Concurrently the paw EMG signal increases, while the actual displacement, as indicated by the movement transducer in the treadmill, lags behind the increases in the other parameters. This same result was in essence obtained in each of the cats.

In addition to these time course analyses we also investigated whether there were significant relations between the value of spectral parameters and steady behavioural states such as 'sitting and waiting for food' (sit), 'eating' and 'walking'. The results of these epoch analyses are shown in Fig. 6. It appears that in all cats the frequency index $I_{PF}$ during walking was higher than during sitting or eating, while for sitting and eating the average $I_{PF}$ was about the same. The amplitude index $I_{AM}$ was generally lower when the cat was eating than when it was sitting or walking. The index of rhythmicity $I_R$ showed no consistent relation with these behavioural states. As expected, all behavioural parameters had low values during sitting and high values during walking, whereas during eating the results were rather variable. This can be ascribed to the differences regarding eating style: some cats had e.g. the habit of manipulating the foodpellets with their forepaws, others took them into their mouth directly. The generally high ACC-values during eating, reflect the fact that the accelerometer placed on the head of the animal was very sensitive to the shocks induced by crunching pellets of dry food. In cat J the average spectral and behavioural

| CAT | Behaviour | $I_{PF}$ | $I_{AM}$ | $I_R$ | ACCH | EMGP | EOG | BOLF | N | $\bar{D}$ | AD |
|---|---|---|---|---|---|---|---|---|---|---|---|
| B | cart ride (r) | 4.90 | .790 | .413 | 145 | 150 | | | 35 | 1.2 | 61% |
| | ride back (b) | 4.73 | .855 | .424 | 68 | 149 | | | 46 | 1.2 | 75% |
| | still in cart (s) | 4.25 | .842 | .423 | 48 | 116 | | | 61 | 0.9 | 60% |
| | eat in cart (e) | 4.33 | .463 | .400 | 254 | 144 | | | 30 | 0.8 | 55% |
| E | cart ride (r) | 4.83 | .578 | .409 | | 185 | 201 | 165 | 24 | 1.4 | 78% |
| | ride back (b) | 4.93 | .616 | .431 | | 115 | 235 | 105 | 46 | 1.5 | 75% |
| | still in cart (s) | 4.04 | .627 | .421 | | 56 | 88 | 87 | 32 | 1.3 | 74% |
| | eat in cart (e) | 4.18 | .512 | .433 | | 431 | 259 | 90 | 27 | 1.1 | 77% |

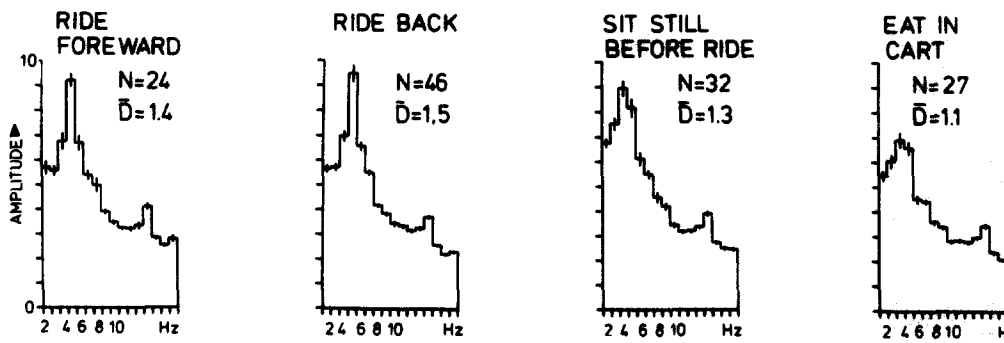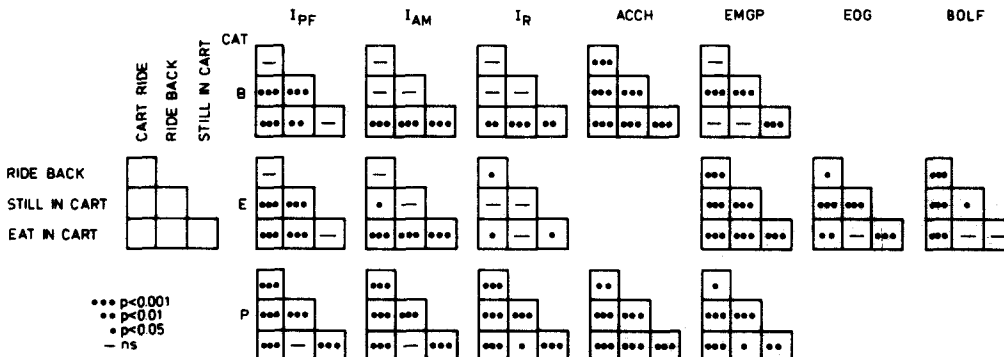| DOG | Behaviour | $I_{PF}$ | $I_{AM}$ | $I_R$ | ACCH | EMGP | EOG | BOLF | N | $\bar{D}$ | AD |
|---|---|---|---|---|---|---|---|---|---|---|---|
| P | cart ride (r) | 5.28 | .857 | .487 | 96 | 136 | | | 20 | 1.8 | 94% |
| | ride back (b) | 4.82 | .709 | .459 | 93 | 130 | | | 35 | 4.8 | 94% |
| | still in cart (s) | 4.17 | .558 | .422 | 74 | 115 | | | 30 | 1.1 | 68% |
| | eat in cart (e) | 4.85 | .790 | .465 | 258 | 120 | | | 22 | 1.7 | 98% |



Fig. 4. Epoch analysis for two cats (B, E) of the value of spectral parameters of the hippocampus EEG, of the integrated bulb activity and of the value of 3 behavioural parameters during periods of 'cart riding' (forwards and backwards), 'eating' and 'sitting still' in the cart. Note the higher index of peak frequency during riding both forwards and backwards as compared to 'sit still' and 'eat' and the relatively low amplitude during eating. For the purpose of comparison an epoch analysis has been provided →
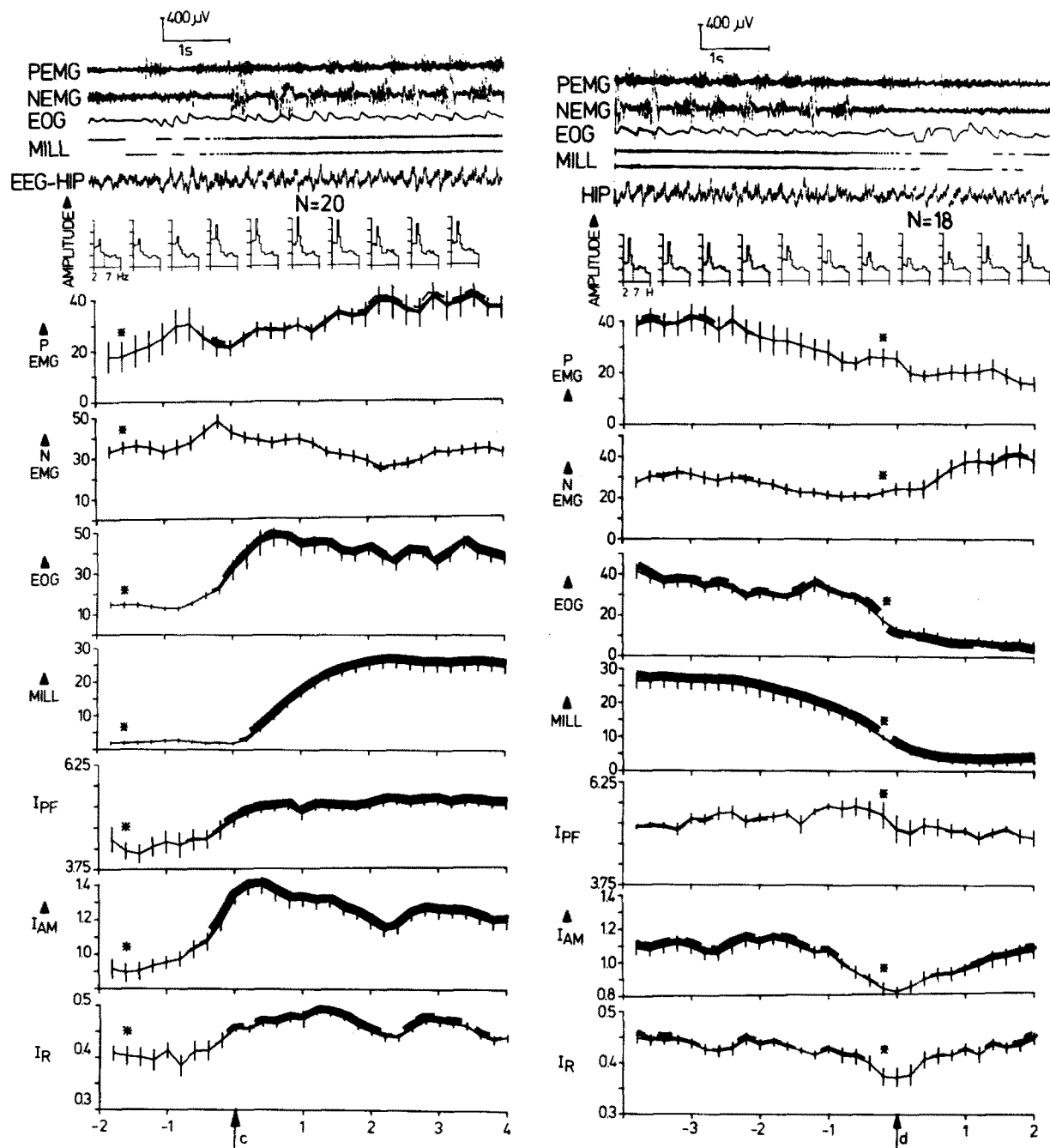
Fig. 5. Time course analysis of the spectral properties of the hippocampus EEG and of the value of 4 behavioural parameters triggered by 'start of walking' (arrow c, on the left panel — 20 realizations) and 'stop walking' (arrow d, on the right panel — 18 realizations). PEMG, paw EMG; NEMG, neck EMG; EOG, electro-oculogram; MILL, output of velocity transducer of classical treadmill; EEG-HIP, hippocampal EEG. Examples of one trial are shown above. (See also caption Fig. 2.)

of equivalent data recorded in dog. These data were derived from the same experimental session used for the time course analysis of cart riding in Arnolds et al.[3]. The values of the EEG and other parameters are statistically compared for the 4 behavioural conditions for two cats and one dog. The box diagrams should be read according to the rows and columns indicated on the example at the left-hand side. The result of the statistical comparison of the average data are indicated as follows: —, no significant difference; * significant difference at $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$. By way of illustration the average spectra of cat E are shown below. Note the narrow peak during cart ride.

| CAT | Beh. state | $I_{PF}$ | $I_{AM}$ | $I_R$ | ACCH | EMGP | EOG | MILL | N | $\bar{D}$ (S) | AD |
|-----|-----------|------|-------|------|------|------|-----|------|----|------|------|
| B | walk | 5.32 | .863 | .408 | 122 | 187 | | | 14 | 0.9 | 33% |
| | sit | 4.00 | .763 | .408 | 67 | 144 | | | 40 | 0.8 | 54% |
| | eat | 4.11 | .463 | .401 | 237 | 197 | | | 22 | 0.9 | 48% |
| E | walk | 5.18 | .173 | .455 | | 270 | 497 | 533 | 24 | 2.2 | 99% |
| | sit | 4.31 | .105 | .427 | | 159 | 116 | 52 | 31 | 1.2 | 70% |
| | eat | 4.35 | .95 | .427 | | 220 | 371 | 38 | 40 | 1.3 | 79% |
| F | walk | 5.15 | .904 | .489 | | 245 | 246 | 476 | 22 | 5.3 | 98% |
| | sit | 4.27 | .868 | .455 | | 116 | 148 | 48 | 11 | 2 | 89% |
| | eat | 4.45 | .427 | .406 | | 125 | 249 | 67 | 13 | 1 | 55% |
| J | walk | 5.21 | .965 | .455 | 214 | 270 | 125 | 393 | 34 | 1.9 | 100% |
| | sit | 4.30 | .946 | .444 | 138 | 68 | 110 | 165 | 45 | 1.4 | 89% |
| | eat | 4.33 | .877 | .483 | 270 | 120 | 122 | 155 | 18 | 1.1 | 100% |
| L | walk | 4.71 | .937 | .443 | 326 | 407 | 216 | 479 | 47 | 1.3 | 82% |
| | sit | 3.51 | 1.026 | .457 | 211 | 336 | 232 | 216 | 30 | 1.1 | 65% |
| | eat | 3.52 | .802 | .444 | 407 | 454 | 229 | 220 | 12 | 0.9 | 37% |
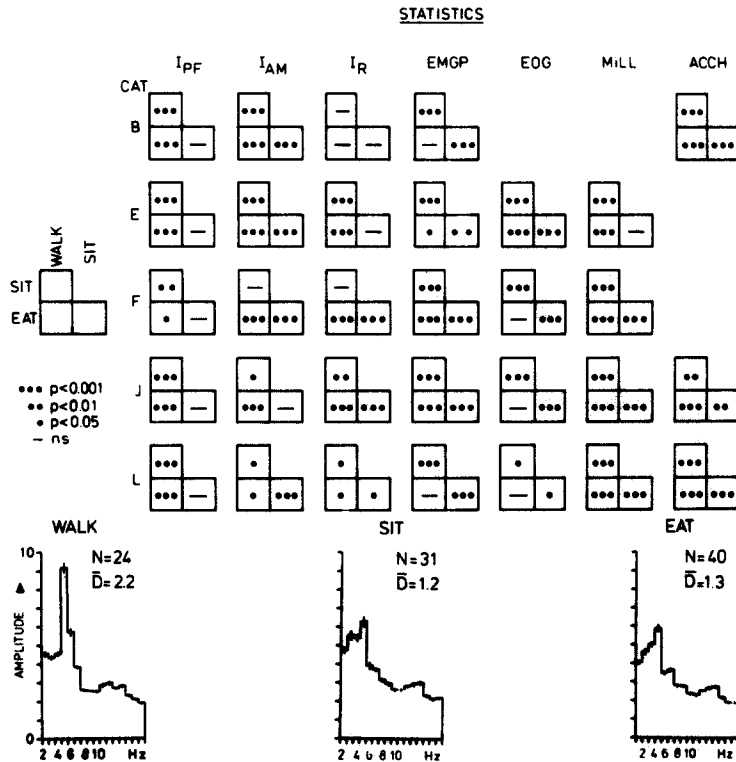


Fig. 6. Epoch analysis of the values of the spectral parameters of the hippocampal EEG and of 4 behavioural parameters, during periods of walking, sitting and eating for 5 cats. Statistical analysis as in Fig. 4. Note the high $I_{PF}$ during walking, as compared to sitting and eating and the low value of $I_{AM}$ during eating as compared to sitting and walking. By way of illustration the average spectra of cat E are shown under the statistical tables.

parameters were calculated for two subsets of walking: the start period and the final period of walking in the treadmill. The $I_{PF}$ was significantly higher during the starting than during the final periods. The same was true for the output of EMG, ACC and MILL; the EOG values and the other spectral parameters did not differ significantly.

*Experiment 4: conveyor belt walking at different speeds (walking with minimal translation)*

Since in the dog a clear-cut relationship between walking speed and RSA characteristics was found[3] it was investigated whether this applies in the same way to the cat.

*Procedures*

Cats E and L were trained to walk on a conveyor belt. The apparatus was enclosed by plywood walls. Only the front consisted of plexiglass. The inside was illuminated by two fluorescent tubes of 40 W each. The conveyor belt was run at speeds ranging from 0.35 to 1.25 m/s. At each of the speeds investigated the cats were trained to walk in a stable fashion for a period of 10–30 s. After each such period of stepping, the animal obtained a reward, consisting of a few pellets of dry food from a food dispenser. The observer regulating the belt speed and the administration of rewards was sitting in front of the transparent side-wall visible to the cat.

*Results*

None of the cats trained on the conveyor belt showed 'automaton-like' stepping, so easily elicited in the dog. The cats were easily distracted by outside events, especially at lower belt speeds. Only periods of smooth uninterrupted walking were used for analysis. The values of $I_{PF}$ were consistently (about 0.2 Hz) lower during conveyor belt walking than during walking in the 'classical' treadmill. In the range of walking speeds investigated a consistent relationship between spectral parameters and walking speed could not be established, despite the fact that a monotonous rise of the values of the behavioural parameters with increasing speed was observed.

In this experimental situation we also investigated whether relationships could be established between the hippocampal EEG pattern and single steps. In cat L a significant modulation of $I_{PF}$ with stepping was found. $I_{AM}$ and $I_R$ did show periodic variations along with the stepping frequency as well, but these were not, or barely, significant (Fig. 7). The trigger used for the analysis as shown in Fig. 7 was when the right forepaw touched the ground. Hence the relation described is rather between step cycles and EEG.

DISCUSSION

In general terms, we can state that in the cat, the relationship between RSA and motor behaviour follows the same pattern as in the dog or the rat. As regards the degree of similarity between cat and dog, the results may be grouped in 3 categories:

(1) Those aspects which showed close similarity between both species; this was the case for the changes in all spectral indices ($I_{PF}$, $I_{AM}$ and $I_R$) in relation to start and stop walking and for the characteristics of these parameters during periods of walking, eating and sitting. In both species during walking $I_{PF}$ reached the largest values, whereas $I_{AM}$ was larger during walking and sitting than during eating. In both species too $I_{PF}$ was larger during walking overground than on a conveyor belt type treadmill.

(2) A number of behavioural acts were correlated in the dog with an increase of all spectral indices ($I_{PF}$, $I_{AM}$, $I_R$), while in cat a *dissociation of spectral indices* was found. These behaviours were the following: the response to riding on a cart (passive translation) and stepping. As regards the first behaviour only $I_{PF}$ increased in cat, whereas $I_{AM}$ decreased and $I_R$ changed little; during stepping only $I_{PF}$ showed a significant modulation.

(3) There were also some behavioural conditions which showed clear correlates with EEG spectral parameters in one species, but not in the other. This was the case with walking at various speeds on a conveyor belt. In dog a slight increase in $I_{AM}$ and $I_{PF}$ was related to higher stepping speeds, but no significant changes were found in
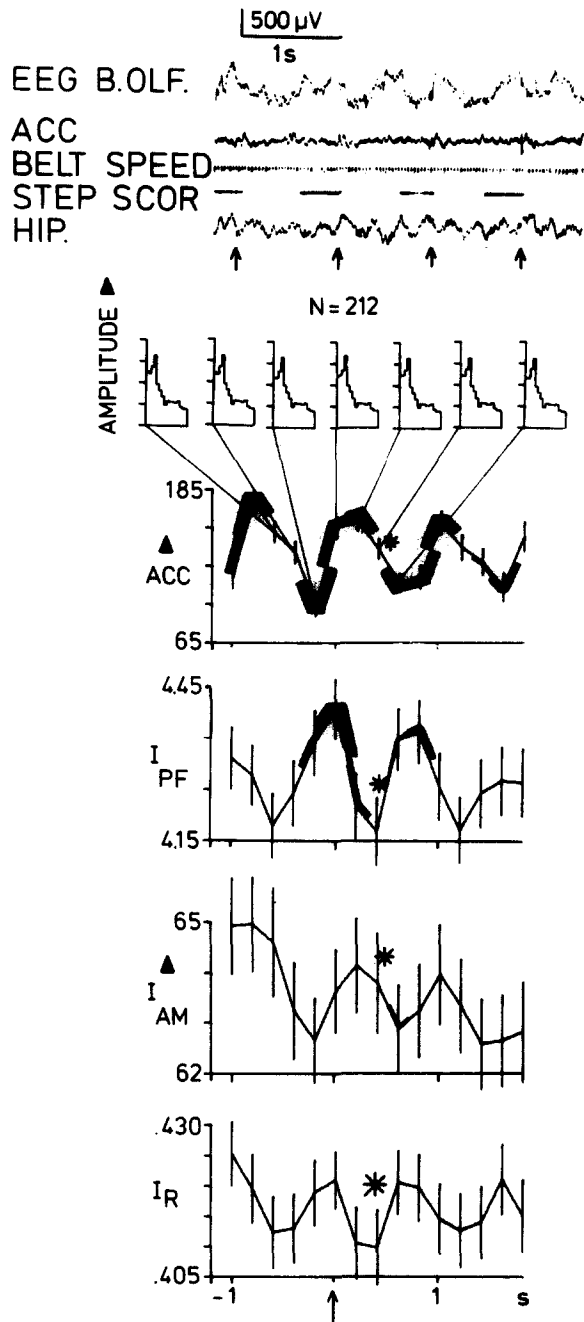
Fig. 7. Time course analysis of the spectral properties of the hippocampal EEG and of the value of the accelerometer, triggered by 'single steps' on the conveyor belt. EEG B.OLF, olfactory bulb EEG; ACC, output of accelerometer on cat's head; Belt speed, output of speed transducer on conveyor belt; STEP. SCOR, manual scoring of the right foot fall; HIP., hippocampal EEG. Note the periodic, step cycle-related variation in the spectral parameters, mainly in $I_{PF}$.

cat. In contrast there was an increase in $I_{PF}$, $I_{AM}$ and $I_R$ in cat related to PGO waves whereas in dog we were not able to find such a clear relation; nevertheless Storm van Leeuwen et al.[28] reported that PGO waves (in this case called lambda waves) in the dog can show phase locking to hippocampal theta waves.

It should be emphasized that the differences noted in 2 and 3 correspond to quite different patterns in the raw EEG records. This may easily give rise to different visual interpretations as occurs in the literature.

In essence the most conspicuous difference between dog and cat lies in the fact that in relation to some behavioural acts there is a dissociation between the changes in the different spectral indices in cat but not in dog. In these cases, in cat, an increase in $I_{PF}$ was not accompanied by a similar increase in $I_{AM}$ and $I_R$. We think, however, that the differences may be resolved on the basis of the simple model formulated below:

The 'septal pacemaker' for the hippocampal RSA is activated by series of action potentials from the brainstem[1]. The higher the impulse density, the higher the RSA frequency[20]. At very high input strengths the relationship breaks down. First the amplitude drops while the RSA peak frequency is high; at even higher input densities a complete desynchronization follows. In our view this should be equated with the small amplitude irregular activity, (SIA), so named by Vanderwolf et al.[31]. This relationship between input density and spectral parameters has been pictured for the cat in Fig. 8.

In this model there are a number of critical values that may vary from species to species: (a) the range of frequencies that the septo-hippocampal system is capable of producing, in particular the frequency at which RSA turns into SIA; (b) the levels of the input density at which 'amplitude saturation' and 'amplitude decrease' start to occur; and (c) the slopes of $I_{PF}$, $I_{AM}$ (and also $I_R$) as function of a global input 'brainstem pulse density'.

We assume that depending on species, different $I_{PF}$ and/or $I_{AM}$ may result from a certain input pulse density. The present results show, indeed, at the start of passive translation (Fig. 3) in cat a
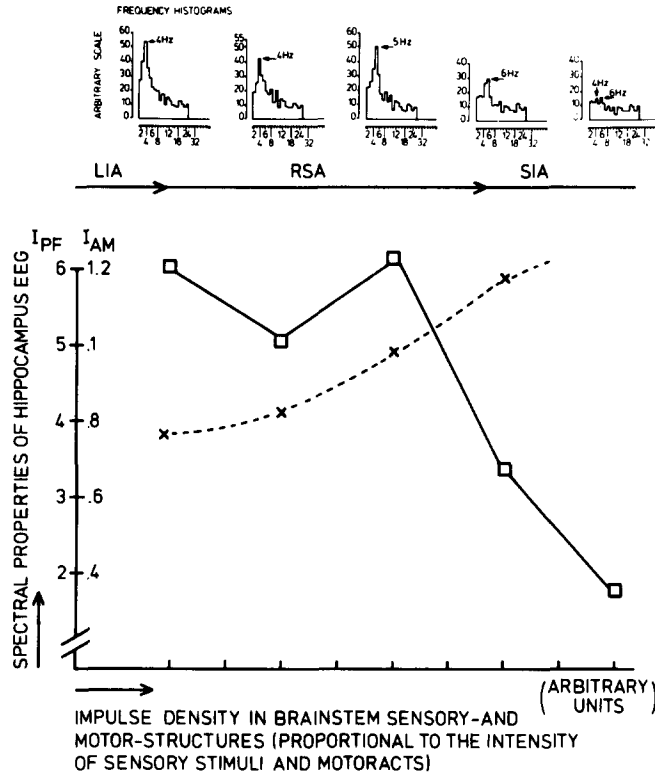
Fig. 8. Schematic representation of the relation between 'impulse density in brainstem sensorimotor structures' and two RSA spectral parameters ($I_{AM}$ and $I_{PF}$). $I_{AM}$, squares and full line; $I_{PF}$, crosses and broken line. The spectra in the top part of the figure are redrawn from ref. 20; they show the effect of stimulation at increasing pulse densities of the lateral hypothalamus upon the hippocampal EEG. The horizontal scale represents a theoretical integrated impulse density reaching the septohippocampal system, in arbitrary units. These values have been extracted from the intensity of the stimulating pulses applied to the diencephalon in the experiments of ref. 20. Note the occurrence of SIA at higher impulse densities.

RSA pattern characterized by an increased frequency ($I_{PF}$) with a decreased amplitude ($I_{AM}$), thus an RSA pattern approaching SIA. In dog, however, in the corresponding behavioural situation the RSA pattern is still far from reaching the SIA pattern.

From the present study it emerges that in the cat evident behavioural correlates of hippocampal RSA are related to vestibular inputs (e.g. passive and active body translation) and/or to eye and neck movements in response to sensory cues. The effect of linear acceleration on RSA both in dog[3] and cat is remarkable. Also in rabbit, Whishaw[36] has shown a correlation between phasic vestibular inputs and RSA frequency shifts.

Another aspect which has to be noted in this context is that some brainstem regions are much more effective in generating RSA than others.

Species differences in this respect are doubtlessly important in explaining the differences described above.

For example in one respect species differences between rat and cat have been signalled: stimulation of the locus coeruleus (LC) in the rat does not produce hippocampal RSA[24,33] whereas in the cat it does[19]. In contrast, stimulation of the caudal pons in the cat elicits hippocampal desynchronization[19], whereas in the rat it produces RSA as indicated above. Since the neurons of the LC respond to sensory stimulation[14] it was suggested by Vertes[33,34] that in the cat the LC could be the area most involved in hippocampal RSA which would then be best correlated to orienting reactions to sensory stimuli[5,10]. It should also be stressed that a strict dissociation of the sensory (input) and the motor (output) aspects of

behaviour is by the sheer nature of free behaviour virtually impossible to obtain.

The hippocampal EEG reflects, in our view, in all species in non-specific terms the degree of neuronal activity in a number of (not necessarily the same) brainstem structures receiving different inputs related to motor *and* sensory phenomena. This consideration alone suffices to abstain from attempts to find at a high level of behavioural integration, e.g. learning, conditioning, arousal, habituation, emotional state, the correlate of RSA common to all species.

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